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With Two Plates

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I. Introduction

The study of the color changes in elasmobranch fishes has been much handicapped by the relatively large size of these animals and the consequent difficulty in keeping them in laboratory tanks and other containers during protracted study. In this respect the young or so-called pups of the viviparous smooth dogfish, *Mustelus canis*, are much more favorable for investigation than are the adults. These young, born during the brief summer period for this species at Woods Hole, have a convenient length of some 25 to 30 centimeters and even at birth are endowed with a fully active melanophore system responsive in its color changes to a degree even beyond that of the adult (Parker, 1936b). They are, moreover, unusually hardy and recover from operation with success. Hence they are a most satisfactory elasmobranch for study. In the following paper a number of the aspects of color change in these young fishes will be discussed, aspects that can be approached much better in them than in the adults.

The work herein recorded was carried out at the Oceanographic Institution in Woods Hole on material supplied for the most part by the Marine Biological Laboratory of that place. The investigations were greatly facilitated by the use of two large open-sea fish-cars 15 by 15 by 4 feet, so built that they could withstand reasonably rough water. They were supported by floats and attached to the inside of the pier of the Oceanographic Institution, where an excellent circulation of sea-water was to be had. The cost for the construction of these cars was defrayed by a grant from the Permanent Science Fund of the American Academy of Arts and Sciences. To the officers of this Fund and to those of the two Laboratories named I am under great obligation for hearty coöperation and assistance.

II. Methods

No special methods were employed in this study. The pups, before they were operated upon, were stupefied by immersion for ten or more minutes in a mixture of sea-water and ice, a method which may be variously modified and which has many advantages for cold-

blooded vertebrates (Parker, 1938). In most experiments the pups were tested in one of two large sea-water tanks in the basement of the Oceanographic Institution. These tanks measured 4 by 4 by 2 feet and were painted inside, one white and the other black. They were illuminated continuously by overhead, 100-watt, electric lights. The black tank could be covered by a movable black roof by which it could be rendered fully light-proof. Both tanks were provided with an ample and continuous supply of fresh sea-water.

III. Blinding

The adult smooth dogfish, when blinded, follows the general rule for the majority of chromatic vertebrates (Parker, Brown, and Odiorne, 1935) and because of the expansion of its melanophores, assumes a dark tint (Parker and Porter, 1934). In this respect it differs somewhat from other elasmobranchs. In eyeless *Raja brachiura*, according to Hogben (1936), the melanophores are neither fully expanded nor fully contracted, and in the related batoid *Urolophus* no color change could be discerned by Griffiths (1936) during the four hours that followed enucleation. In *Torpedo marmorata* Veil and May (1937) observed that the usual brownish tint of this species was maintained unchanged as well without the eyes as with them. Possibly some of these negative results may disappear when means have been devised for the better handling of these fishes. But whatever such final results may be on other elasmobranchs the adults of *Mustelus canis* on the loss of their eyes darken so quickly and so regularly that this change must be attributed to the blinding of these fishes.

The normal pups of *Mustelus*, like the adults, take on tints fully pale or fully dark according to their illuminated environments. These changes occur somewhat more rapidly in the pups than they do in the adults. They ordinarily take place in a relatively few hours, the change to the dark condition being accomplished in less time than that to the pale one.

In the initial experiments six pups, which were known to be fully capable of color change, were blinded by having their optic nerves cut. This operation was easily accomplished by buccal incisions. The pup after stupefaction by cold was held ventral side up and with the mouth widely open. The points of a pair of small scissors slightly separated were pressed through the membrane and cartilage on the roof of the mouth and into the rear of the orbit so as to include between the blades the optic nerve as it leaves the eye-ball. By a single cut of the scissors this nerve could be easily severed and after

a similar operation on the opposite side of the head the pup was assumed to be completely blinded. Such operations were almost bloodless. The operated pups on recovery swam normally except that they collided continually with the walls of the tank or with other obstacles showing that they were in reality without vision.

Of the six pups thus treated three were put in the large, white-walled illuminated tank and three in the black-walled one. After half a day the two sets of fishes were compared. In both sets the individual pups were obviously dark as attested not only by ordinary inspection, but also by the state of their melanophores as seen under the microscope (Fig. 4). The two sets were, however, indistinguishable and both were much darker than normal pale pups in the white-walled tank (Fig. 2), but not as dark as normal dark ones in the black-walled tank (Fig. 1). I never saw blinded pups reach so deep a tint as was occasionally observed in blinded adults (Parker and Porter, 1934). The blinded pups were nevertheless always to be classed as dark individuals and the fact that the two sets, one in white and the other in black surroundings, were indistinguishably dark shows, as might have been expected, that the eyes are essential for responses to environmental illumination.

The six blinded pups were now redistributed in that three were put in the white-walled illuminated tank, and three in the tank from which all light was excluded. After seven hours it was obvious on quick inspection that the three pups in darkness were all somewhat paler than any of those in the illuminated tank, a condition that was still somewhat more striking after twelve hours when both to the unaided eye and under the microscope (Fig. 3) the blanching of the blinded pups in darkness was obvious. A cut was now made in the pectoral fin of one of each of the two sets of pups and in half an hour a band of maximum paleness had appeared on each fin. Thus a cut in the fin of a blinded pup may produce a local maximum blanching like that which occurs over the whole of a normal pup with functional eyes and in illuminated white surroundings. In this respect the cut may be said to be a substitute for the eye.

As a final step in this series of tests the three blinded pups that had been kept in darkness were now transferred to the white-walled illuminated tank and those that had been in the illuminated tank were placed in darkness. After five hours the three pups in darkness were all found to be paler than those in the light, the two sets having thus reversed their tint with the change in illumination. From this observation it is evident that blinded *Mustelus* pups have not entirely

lost their power to change in tint, for they are consistently darker in bright light than in darkness.

The effect of the pituitary gland on these color changes was next taken up. The buccal operation by which Lundstrom and Bard (1932) removed the pituitary complex from the adult *Mustelus* through an aperture cut in the cartilage of the roof of the mouth is very easily applied to the pup. By this procedure the pituitary glands were excised from four pups and these young fishes were then put two in a dark-walled illuminated tank and two in a white-walled one similarly lighted. Both sets of pups gradually blanched and after twenty hours both reached what appeared to be maximum paleness. When their pectoral fins were inspected under the microscope, the melanophores of these parts were found to be fully punctate (Figs. 5 and 6), and it was obvious that their pigment could undergo no further concentration. I therefore assumed that their melanophore pigment had reached a state of complete concentration and that this state was dependent upon the absence of the pituitary gland and independent of the nature of the illuminated environment. Two of these hypophysectomized pups were then put in complete darkness and two in the white-walled illuminated tank. After seven hours these two sets of pups were still maximally pale and indistinguishable. The optic nerves of all four fishes were then cut by the operation already described and the pups were set aside in the black-walled tank for inspection. At this stage one of the pups escaped from the tank during the night and died on the floor of the tank room. The remaining three, however, were kept in the tank and under inspection for over a day and during this time they all persisted in remaining fully pale. At the end of this time the test was judged concluded though the experimental fishes lived three to four days longer. During this final period cuts were made in some of their uncut pectoral fins with the results that no pale bands whatsoever appeared. The skin in these fishes was apparently fully pale before the cuts were made and was not open to further blanching. This question was tested further by removing the pituitary glands from two new pups and, after about a day when the pups had become very pale, by cutting their pectoral fins. The regions where bands might have appeared were, however, not paler than the rest of the fish showing that the loss of the pituitary gland was in itself sufficient to induce maximum blanching.

It is well established that a smooth dogfish blanched by hypophysectomy can be darkened temporarily by the injection of an extract from the intermediate lobe of the pituitary gland (Lundstrom and

Bard, 1932; Parker and Porter, 1934). The activating substance contained in this extract and commonly designated as intermedin is believed to be the normal means of darkening the fish. The control of this substance must be dependent upon the fish's eye. When the retinal field of the fish is stimulated by light from an environment of dark coloration, the activating substance is liberated from the gland and when the field is stimulated by light from whitish areas, the discharge of this special material is inhibited. These responses can be shown to occur in the pups as they do in the adults. It has been further pointed out in this paper that pups in which the pituitary glands are still intact, but which have been blinded by the severance of their optic nerves, are quite dark in bright light and not so dark in darkness. So far as is known, these changes depend upon the activity of the pituitary gland, for they disappear with its loss. Since they occur in blinded pups, they imply the action of some other receptor than the eye. That they do not depend upon some hormone given out by the eyeball itself, such as has been found by Kropp (1929) in certain melanophore reactions in tadpoles, is seen in the fact that they occur as well in enucleated pups as in those blinded by the simple severence of the optic nerves. But where the activating receptors are to be found I have been unable to discover. Somewhere in the body of *Mustelus* there must be receptors which, when stimulated by light, induce a discharge of intermedin and when enveloped in darkness inhibit that discharge, or in some other way induce these mild responses. In this respect *Mustelus* appears to be in the same category as certain other vertebrates such as the minnow *Phoxinus* (von Frisch, 1912; Scharrer, 1928), the catfish *Ameiurus* (Abramowitz, 1936), possibly the lamprey (Young, 1935) and even the frog (Rodewald, 1935).

IV. Blanching

The blanching of elasmobranchs, as Waring (1936) remarks, is far from being fully understood. Adrenalin, one of the most universally effective agents in the concentration of melanophore pigment, was found by Young (1933) to be without influence on the tints of *Scyllium* and of *Torpedo*. Wykes (1936) obtained from this agent only a slight blanching in *Raja* and *Rhina*. *Mustelus* on the other hand blanches readily to adrenalin (Lundstrom and Bard, 1932: Parker and Porter, 1934; Parker, 1935b, 1936a, 1936b), though from the very heavy dosage necessary for this effect it is doubted by some workers (Lundstrom and Bard, 1932) whether this response may not be due to vasomotor changes rather than to a direct influence on the melano-

phores. The fact that the defibrinated blood from a pale *Mustelus* is without effect when injected under the skin of a dark one (Parker and Porter, 1934) makes it probable not only that adrenalin is not normally concerned in the blanching of this dogfish, but also that any blood-borne agent such as the W-substance hypothesized by Hogben (1936) for the blanching of certain other elasmobranchs, does not occur in *Mustelus*. Thus far the only known normal method of blanching for *Mustelus* is that dependent upon concentrating nerves (Parker and Porter, 1934), a method which appears to be peculiar to this dogfish, for, up to the present, it has not been found to any extent in other elasmobranchs.

The nervous blanching of *Mustelus* has been shown to be due to an oil-soluble hormone, a lipohumor, produced by the concentrating melanophore nerves of this fish (Parker, 1935b, 1936c). Is it not possible that this animal possesses other means of becoming pale than that just mentioned? *Mustelus* like most other fishes dies pale, a condition which is generally attributed to the lack of available oxygen for the melanophores when the circulation of blood ceases. This, however, is not likely to be a natural means of blanching, though it is conceivable that by vasomotor disturbances it might play a part in inducing such a change. Much more probable as a means of blanching would be the removal from the fish's blood of the pituitary secretion by which the dispersed state of the melanophore pigment was induced.

For experimental tests of this question *Mustelus* pups are especially well adapted. If a strong cord is tied firmly and tightly around the head of a dark pup at the level of the posterior margins of the eyes and another at the level of the vent, the pup will be divided into three regions: an anterior one which in consequence of the ligating cord is without circulation, a posterior one also without circulation, and a middle region containing the heart and connecting vessels, and in which in consequence of the presence of these organs a circulation of blood still goes on. A dark pup so divided will remain dark for a full hour. If in a freshly ligated pup the pericardium, which is of course in the middle region, is opened and an irrigation canula is tied into the ventral aorta, the middle region can be washed free of blood in some five minutes by a current of Ringer's solution. During the washing this region blanches very completely and remains so indefinitely (Fig. 7). This test was made on four pups and always with the same result. Under the microscope the melanophores of the middle region could be seen to be reduced almost to the punctate state (Fig. 9), while those of the anterior and the posterior regions remained

with dispersed pigment (Fig. 8). Plainly the washing out of the blood with its contained intermedin from the middle region is the occasion of its blanching.

That this blanching is not due to the death of the tissues concerned is seen in the fact that when a middle region blanched in the way described is further irrigated with a mixture of one volume of Ringer's solution and two volumes of commercial pituitrin, this middle region again darkens in about a quarter of an hour through the dispersion of its melanophore pigment. Hence I conclude that *Mustelus* may blanch in consequence of the loss of the pituitary dispersing neurohumor. Since it also blanches through nerve action and in death, this fish may be said to possess three ways of accomplishing this end. The illumination of the retina with light from a pale tinted environment probably not only excites the concentrating nerve fibers to produce their appropriate neurohumor, but it may also inhibit the discharge of the dispersing neurohumor from the pituitary gland.

The melanophores of a denervated area on a blinded, hypophysectomized *Mustelus* in darkness would seem to be as near freedom from stimulation as could easily be imagined. In fact, in discussing this condition in *Ameiurus* Abramowitz (1936) with a certain degree of caution has called attention to exactly this state as one devoid of stimulation. Such an interpretation would seem quite reasonable except for the fact that in *Mustelus* the state just described leads to a condition of complete concentration of melanophore pigment (paleness), whereas in *Ameiurus* it induces precisely the opposite state (dark coloration). If, as Abramowitz suggests, it is the property of an unstimulated melanophore in *Ameiurus* to disperse its pigment nearly to fullness, it must be admitted that it is the property of a *Mustelus* melanophore under like conditions to concentrate its pigment. The understanding of such a situation is by no means easy. It is conceivable that all cells called melanophores are not really alike, an opinion for which much might be said. It is also possible that we have not yet exhausted all the sources of stimulation and that *Mustelus* and *Ameiurus* in the conditions described illustrate the action of certain opposing activators as yet undiscovered. These conditions come very close to the problem formerly discussed for chromatophores concerning states of rest and of activity. What are to be described as these states in chromatophores I have elsewhere analyzed (Parker, 1935c) and I still see no reason to change my opinion that it is best to describe the active chromatophore as one in which the pigment is moving and the resting one as one in which the

pigment is quiescent. Certainly melanophores whose nerves have been recently cut and whose pigment is in consequence dispersed are not in a state of paralytic rest as was at one time believed (Parker, 1936c, 1936d). Hence I hold to my former view as to rest and activity. Though it is perhaps premature to make a decision, I am inclined to look upon the conditions of the melanophores in *Mustelus* and in *Ameiurus* just described as due to novel and thus far undiscovered means of stimulation rather than to innate and fundamental differences of type in their organization.

V. The Nervous Control of *Mustelus* Melanophores

Mustelus is peculiar among elasmobranchs in that its pale phase is under the control of nerves. This was first demonstrated by Parker and Porter (1934) in a series of experiments in nerve cutting. Whenever a cutaneous nerve in this dogfish is cut a blanched area corresponding to the peripheral distribution of the nerve in question appears. In place of the excitation supplied by a cut, faradic stimulation will also induce peripheral blanching (Parker, 1935a). In these tests, however, nerves were not freed and directly stimulated, but the electric current was applied to the tissue through which the nerves passed. In pups it is possible to expose just dorsal to the pectoral fin the nerves of the brachial plexus and a single one of these can be lifted and placed under the electrodes of an induction apparatus. In a dark pup so prepared no color change occurs until the current is made when, after some fifteen minutes of stimulation, a faint irregular pale area will develop in that part of the fin to which this particular portion of the brachial plexus is distributed. This area is by no means so well defined nor so fully pale as that produced by cutting nerves nearer the periphery of the fin, but its presence is unquestionable and its position appropriate. Its partial vagueness is due undoubtedly to the irregular spread of the nerve fibers in the particular branch stimulated as compared with the more regular and limited distribution of the smaller branches which are severed by a peripheral cut in the fin. Electric stimulation applied to a nerve in the brachial plexus of a fully pale dogfish pup is followed by no observable color change in the fin. Thus faradic stimulation applied to an isolated nerve in a dark pup results in the same general effect, blanching, as the cutting of nerves in the fin does. This conclusion is at first sight not in agreement with that of other workers who have attempted the electric stimulation of melanophores and their nerves in elasmobranchs. Schaefer (1921) was not able on the application of faradic

stimulation to the skin of *Raja clavata* to elicit responses from its melanophores. Nor was Wykes (1936) successful in obtaining a response on applying a similar stimulus to the spinal nerves, haemal arches, and skin of *Raja*, of *Rhina*, and of *Scyllium*. But in none of these fishes is there any reason to suppose that the melanophores are subject to nervous activation. In fact there is very good ground for assuming that they are not so controlled and if this is true, it is very improbable that electric stimulation of nerves distributed to a given area would have any effect whatever on the melanophores of such an area.

In contributions recently published on the antidromic responses in *Fundulus* (Parker, 1936e, 1937a) I have shown that the melanophore nerve fibers when stimulated by a cut not only excite the melanophores distal to the cut, but also activate those proximal to it. This antidromic action was to be expected though evidence of it is not always easily discoverable. In the various experiments on *Mustelus* pups I attempted repeatedly to test these fishes for antidromic responses, but my efforts were invariably unsuccessful. Though for tests of this kind *Mustelus* would appear to be more favorable than *Fundulus*, I have been unable to carry such tests to a successful issue. Nevertheless I am convinced that in *Mustelus* antidromic action ought to be demonstrable.

In 1935 and in 1937 I showed that an ether extract of the fins and skin of pale smooth dogfishes yielded a material that when injected under the skin of a dark fish excited in it a pale spot due to the concentration of pigment in the local melanophores. The effective material in this extract was found to be soluble in olive oil and in ether, though not in water, it would withstand heat to 110° C., boiling with weak alkali and with weak acid. It was therefore shown to be a relatively stable substance. In the summer of 1936 I collected a considerable quantity of pale *Mustelus* fins and skins and kept them in glass over the period of a year. At the beginning of this season (1937) I extracted a reasonable amount of these skins and fins and under appropriate conditions I injected some of this extract under the skins of several dark *Mustelus* pups. They all showed characteristic secondary blanching (Fig. 10) and thus demonstrated the efficiency of the extracted substance even after a year's standing. These observations confirm the opinion already expressed that this *Mustelus* lipohumor is a fairly stable substance.

Having prepared this crude extract in some quantity, I proceeded to test it on other vertebrates, namely on the catfish, *Ameiurus*

nebulosus, and on the common frog, *Rana pipiens*. In both instances three dark individuals and three pale individuals received in each case 0.05 cc. of the crude oily extract mixed with an equal volume of Ringer's solution and shaken into a coarse emulsion. In *Ameiurus* this mixture in proper amount was injected under the skin of the flank of the fishes on their right sides, and in a corresponding position on their left sides an equal amount of Ringer's solution was introduced as a control. Similar injections were made under the skin of the calves of the six frogs, the emulsion into the right calves, and the Ringer's solution into the left ones.

The three pale catfishes were kept in a white illuminated vessel and remained unchanged for about an hour after the injection had been made, when a well marked dark spot appeared in the skin of each fish directly over the region of injection. These spots persisted for about three and a half hours, when one of the catfishes was preserved in formol-alcohol as a demonstration (Fig. 11). No marks of any kind appeared over the regions into which only Ringer's solution had been injected. The two catfishes still living were then injected each with 0.2 cc. of adrenalin 1 : 1000. In a little less than an hour both fishes were very pale and the dark spots originally on them had fully disappeared. Four hours after the injection of the adrenalin and presumably after it had disappeared from the blood of the fishes, the dark spots returned to view, partly but unmistakable. In twenty-four hours all traces of them had fully disappeared.

The dark catfishes retained in a black-walled vessel were, after an hour, still fully dark, nor were there any changes to be noted over the regions of injection of the extract or of the Ringer's solution. They were then put into a white-walled vessel where they slowly blanched. Seven hours after this transfer the three fishes were noticeably pale, but without evidence of dark spots. The next morning thirteen hours after the last record, all three were fully pale with faint but unquestionable dark areas over the regions injected with extract, but not over those injected with Ringer's solution. In a day dark areas on these fishes had disappeared. I had not enough crude extract to repeat these tests, but in consequence of their uniformity and definiteness, I think it fair to conclude that crude extract from pale smooth dogfishes contains a substance that darkens *Ameiurus*.

The three pale and three dark frogs that were injected with pale dogfish extract and Ringer's solution yielded much the same results as the catfishes did. In all instances the extract produced a faint but unmistakable darkening of the calf of the pale frog and no noticeable

change in that of the dark frog. The dark reaction was by no means so pronounced as that in the catfish, but it was unmistakable. In all instances the injected Ringer's solutions was without effect on the tint of the calf. It is a surprising fact, but nevertheless a certain one, that the crude oily extract from a pale *Mustelus* which will produce a pale spot on another *Mustelus* will produce darkening in *Ameiurus* and in the frog. It cannot of course be said that it is the same substance that produces these opposite effects, for the crude extract from the dogfish may contain one substance which blanches a dark dogfish and has no effect on the catfish and the frog and another which has no effect on the dogfish and yet darkens the catfish and the frog. Only future work can settle this question, but it is interesting that a single crude extract should excite these opposite effects.

VI. Summary

1. The adult smooth-dogfish, *Mustelus canis,* when blinded, takes on a dark color. Blinded pups of this species are also dark irrespective of a white or a black illuminated environment.

2. Blinded pups in darkness are paler than blinded pups in the light. The darker tint of the pups in the light is due to a pituitary secretion, for it is replaced by full blanching when the pituitary gland is removed.

3. In blinded pups the pituitary gland does not discharge intermedin when these fishes are in the dark; it does discharge a very small amount when they are in the light. The receptor for this light response was not discovered.

4. Blanching in *Mustelus* can be artificially excited by adrenalin. There is no evidence that it is naturally excited by any blood-borne agent such as the W-substance hypothesized by Hogben. Blanching in *Mustelus* is due to a nerve-produced lipohumor, by a loss of intermedin from the blood, and by anoxemia.

5. The concentrating melanophore nerve fibers in *Mustelus* gave no evidence of antidromic response.

6. The crude concentrating lipohumoral extract from *Mustelus* after a year's retention in the dried state is still effective as a blanching agent for this dogfish. It induces darkening in *Ameiurus* and *Rana.* This rather remarkable response may be due to another substance contained in the crude extract than that which caused the blanching of *Mustelus.*

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DESCRIPTION OF FIGURES

All figures except number 11 are photographs from the smooth dogfish *Mustelus canis* adults or pups. I am under obligation to Dr. F. M. Carpenter for the preparation of these photographs.

Plate 1

All figures on this plate are from melanophores on the dorsal side of the pectoral fins of dogfish pups.

Fig. 1. Melanophores with fully dispersed pigment as seen in the dark phase of the dogfish.

Fig. 2. Melanophores with fully concentrated pigment as seen in the pale phase of this fish.

Fig. 3. Melanophores from a blinded dogfish in darkness. The pigment is more concentrated than in a similar fish in the light (Fig. 4).

Fig. 4. Melanophores from a blinded dogfish in light. The pigment is less concentrated than in a similar fish in darkness (Fig. 3).

Fig. 5. Melanophores from a hypophysectomized dogfish on an illuminated, black background.

Fig. 6. Melanophores from a hypophysectomized dogfish on an illuminated white background. The pigment under the two conditions shown in Figures 5 and 6 is at full concentration; one condition is indistinguishable from the other.

Plate 2

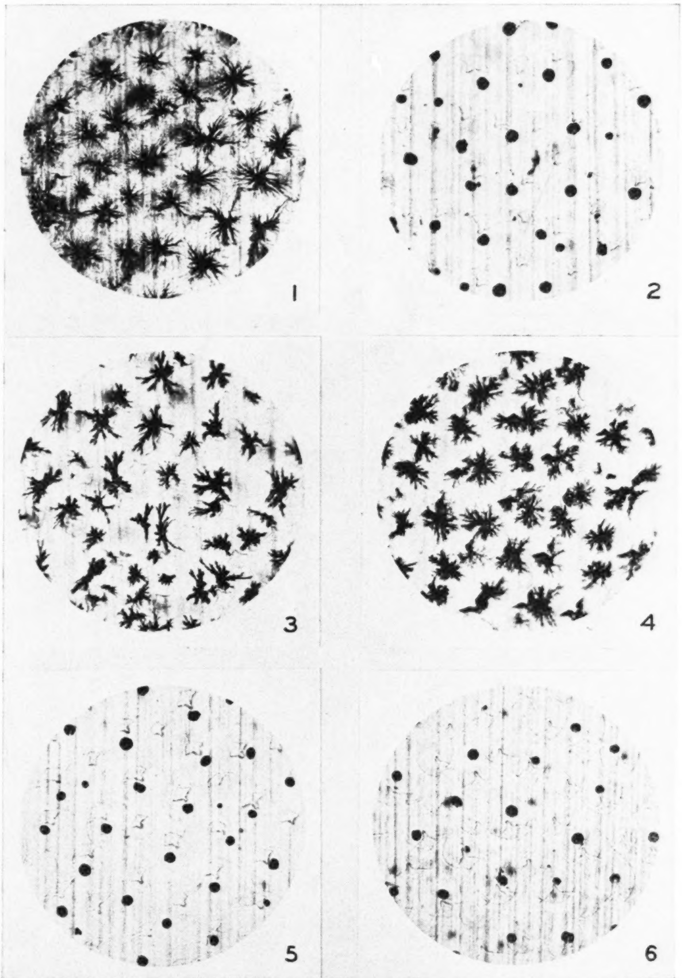
Fig. 7. Dorsal view of a pup originally dark and divided by firm ligatures into three regions, anterior, posterior and central. The central region has been fully irrigated with Ringer's solution from the ventral aorta and has in consequence largely blanched while the anterior and posterior regions have remained dark.

Fig. 8. Melanophores from the dorsal part of the head of the preparation shown in Fig. 7. The pigment in these cells is about fully dispersed.

Fig. 9. Melanophores from the dorsal part of the flank of the preparation shown in Fig. 7. The pigment here is much concentrated.

Fig. 10. Side view of the trunk of a dark pup next the anterior dorsal fin showing a pale spot induced by the injection of an extract from pale dogfishes' skins that had been kept dry in the laboratory for one year.

Fig. 11. Side view of a pale catfish, *Ameiurus nebulosus*, showing a dark spot under the anterior dorsal fin induced by an injection of the same kind of extract that produced a pale spot on a dogfish (Fig. 10).



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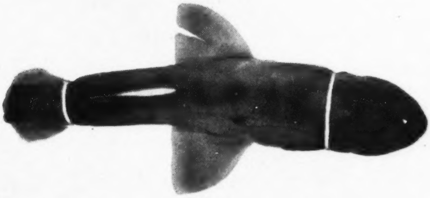

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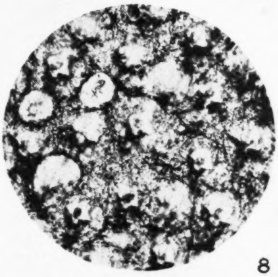

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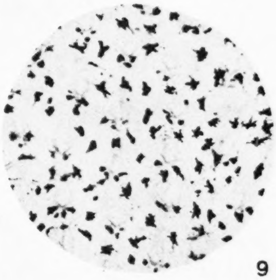

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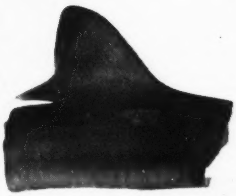

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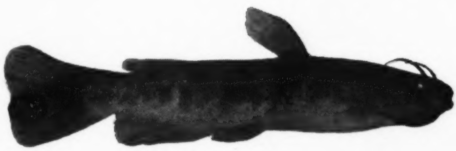

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